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Multiple factors influence the vegetation composition of Southeast U.S. wetlands restored in the Wetlands Reserve Program[1,2]

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De Steven, D. (USDA Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, Stoneville, MS 38776) and J. M. Gramling (Department of Biology, The Citadel, Charleston, SC 29409). Multiple factors influence the vegetation composition of Southeast U.S. wetlands restored in the Wetlands Reserve Program. J. Torr. Bot. Soc. 140: 453–464. 2013.—Degradation of wetlands on agricultural lands contributes to the loss of local or regional vegetation diversity. The U.S. Department of Agriculture's Wetlands Reserve Program (WRP) funds the restoration of degraded wetlands on private 'working lands', but these WRP projects have not been studied in the Southeast United States. Wetland hydrogeomorphic type influences hydrodynamics and thus the vegetation of restored sites, but species composition may also be affected by prior land-condition and restoration methods. We examined the variation in restored wetland vegetation of 61 WRP sites (representing 52 projects) across the Southeast region. Field surveys identified the common plant species at each site, and species composition was analyzed in relation to hydrogeomorphic type and specific restoration methods that were linked to pre-restoration habitat status. At least 380 plant species were recorded across all sites. Site floristic composition generally reflected variation in wetness conditions and vegetation structure. Wetlands restored by 'non-intensive' methods overlapped in species composition irrespective of hydrogeomorphic type, as a consequence of successional dynamics related to natural hydrologic variation. More distinctive species composition occurred in wetlands restored by 'intensive' methods designed to compensate for intense agricultural land-use before restoration. In the Southeast U.S., WRP wetlands are supporting a variety of plant assemblages influenced by hydrogeomorphic settings, site land-use history, and differing restoration approaches.

Key words: Conservation Effects Assessment Project (CEAP), hydrogeomorphic (HGM) classification, vegetation diversity, wetland restoration, Wetlands Reserve Program (WRP).

Wetland degradation caused by drainage and agricultural activity can result in significant loss of vegetation diversity and other ecological benefits such as wildlife habitat and water-quality improvement. In the United States, a mechanism for restoring degraded wetlands on private agricultural lands is the Wetlands Reserve Program (WRP), one of several conservation programs administered by the U.S. Department of Agriculture (USDA). Agricultural uses on such 'working lands' may include row-cropping, pasture, and rangeland grazing. The WRP offers private landowners a cost-share for wetland restoration treatments and also pays for acquiring long-term conservation easements on the restored sites. Easement tracts can include some extent of upland buffer land, and the landowners retain rights to limited uses such as hunting and fishing. By 2008 there were > 10,000 WRP easements on nearly 2 million acres nationwide, mostly in farming-intensive regions, at a total cost of > $2 billion since the

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program's inception in 1992 (NRCS 2009). In light of the large expenditures for the WRP and other USDA conservation programs, the Natural Resources Conservation Service (NRCS) developed the Conservation Effects Assessment Project (CEAP) as a multi-faceted effort to evaluate the ecological benefits of these programs (Mausbach and Dedrick 2004, Duriancik et al. 2008).

The general objective for WRP restorations is to recover wetland hydrologic function, native wetland vegetation, and desired wildlife habitat in relation to programmatic and landowner goals (cf. De Steven and Gramling 2012). The outcomes of the WRP for vegetation composition and wildlife habitat have been studied in the farming-intensive Southern Mississippi Alluvial Valley region (e.g., Twedt 2002 et al., Heard et al. 2005, King et al. 2006, Faulkner et al. 2011). However, in the mixed forested-agricultural Southeast region (Piedmont and Coastal Plain), a CEAP review found that even the basic features of WRP projects were largely unknown (De Steven and Lowrance 2011). The Southeast has a great variety of wetlands and associated plant communities, yet there was little information on which wetland hydrogeomorphic (HGM) types were being restored on program lands. This is relevant for assessing conservation benefits because HGM types represent morphological forms (e.g., depressional, flat, riverine) with different hydrodynamics, which leads to differences in some ecological traits and functions (Brinson 1993, Brinson and Reinhardt 1998). Consequently, a CEAP survey of over 100 WRP restoration projects was conducted in 2010 across several Southeast states (De Steven and Gramling 2012). The project plans were found to encompass four wetland types (depression, flat, riverine headwater, riverine floodplain) and various restoration methods (see below). Aerial imagery indicated that 'prior-habitat' conditions also differed among the project wetlands before restoration, such that some had been in active agriculture whereas others already appeared to be semi-naturally vegetated (including bottomlands that had been timber-harvested). Regardless of wetland type or prior condition, field data indicated that most restorations were successful in providing functional wetland habitats dominated by native wetland vegetation (De Steven and Gramling 2012).

The initial analyses found few differences among wetland HGM types or prior habitats in the generalized attributes that indicated natural wetland vegetation (e.g., high percentages of wetland species and native species) (De Steven and Gramling 2012). However, this does not imply a lack of floristic variety among the restored wetlands. The underlying species composition could vary more widely in relation to multiple factors, including how specific restoration methods were used in relation to HGM type and prior habitat. Nearly all depressions and flats were restored 'non-intensively', i.e., by installing ditch plugs or simple water-control structures to block artificial drainage and by relying mainly on passive revegetation. The methods for riverine wetlands differed with prior-habitat condition. Restoration of timber-harvested floodplains was also 'non-intensive', using simple methods of breaching roads or dikes to promote river flows and allowing forests to regenerate naturally. In contrast, prior-agriculture floodplain and headwater tracts were treated with a more 'intensive' dual-practice approach, usually without reconnection to major river flows. The approach consisted of installing semi-enclosed waterfowl-habitat impoundments on part of the project tract, plus widespread planting of tree seedlings across the remaining area. Impoundments are managed with periodic water drawdowns to encourage seasonal growth of food plants for waterfowl, a system called moist-soil management (Strader and Stinson 2005). Tree seedlings are planted in systematic arrays of multiple species, typically bottomland oaks and other floodplain trees.

This mix of non-intensive and intensive restoration treatments could likely amplify the floristic variation among restored wetlands beyond any influence of wetland type or other factors. In this paper, we describe the species composition of Southeast WRP wetlands in greater detail. We specifically examine whether the interactions between wetland type and the distinctive restoration approaches linked to prior-habitat condition (i.e., moist-soil management, intensive tree-planting) have produced variability in species composition that would not be apparent from considering wetland type alone. The findings provide a general picture of the extent of vegetation diversity among WRP program wetlands across the Southeast region.

Table 1. Features of 52 WRP projects classed by wetland HGM type. Percent wetland area is estimated as the % of easement-tract area (ha) with mapped hydric soils. Project age is years since restoration. 'Prior-agriculture' sites were in row-crops or pasture before restoration.

HGM type	*n*	# prior-agriculture	Easement area (mean ha [range])	% wetland area (mean ± SE)	Project age (range of years)
Depression	14	8	26.7 [4–94]	64 ± 5	2–11
Wet flat ‡	11	5	135.3 [5–779]	64 ± 8	2–11
Riverine headwater	13	6	33.4 [6–167]	83 ± 3	3–8
Riverine floodplain	14	7	149.3 [4–325]	85 ± 5	3–10

‡ includes 3 very large (81–779 ha) 'Carolina bays'.

Materials and Methods. Sites and Surveys. Field data had been collected on a stratified-random subsample of 53 WRP projects chosen from the 109 projects in the CEAP survey (details in De Steven and Gramling 2012). For this paper we excluded one outlier project with recent management disturbance, leaving 52 projects for analysis (Table 1). The projects ranged across three states (South Carolina, Georgia, and 'Coastal-Plain' Mississippi) and multiple sub-regions (Piedmont, Hilly Coastal Plain, Coastal Flats, MS Loess Uplands). Project age (i.e., time since restoration was implemented) averaged six years. Four wetland HGM types were represented: depressions, flats, riverine headwater areas on low-order (1^{st}–3^{rd}) streams, and mainstream floodplains on higher-order rivers. Project (tract) sizes varied widely, partly as a natural consequence of geomorphic difference among HGM types. The project wetlands also had contrasting 'prior-habitat' condition, with about half having been in active agriculture (cropping or grazing) and the rest already appearing more naturally vegetated before restoration (Table 1). The 'prior-vegetated' projects included depressions, flats, and headwaters altered by past ditching and drainage, as well as forested floodplains disturbed by past timber harvest and the associated logging roads.

Field data were collected in July–August 2010 with methods adapted from "routine wetland determination" procedures (ACOE Environmental Laboratory 1987). Each project was assessed with spot-surveys at 1–4 distributed sample locations; number of locations was determined by tract size and cover types (details in De Steven and Gramling 2012). At each location, we traversed a broad area and recorded all dominant plant species in each of four strata (tree, sapling/shrub, herb, woody vine), where 'dominants' were species representing roughly 20% or more of stratum cover by visual estimate. Wetland indicator categories (Reed 1997) were assigned to each species and grouped into three classes based on ACOE 1987 protocols: true 'wetland' species (OBL and FACW categories), 'facultative' species often occurring in wetlands (FAC+ and FAC categories), and 'upland' (non-wetland) species (FAC-, FACU, UPL categories). Wetland and facultative species collectively are 'hydrophytic' and indicate 'wetland vegetation' when they comprise ≥ 50% of all species (ACOE Environmental Laboratory 1987). Species were also classed by growth habit and life history (e.g., herbaceous forb/graminoid, annual/perennial, woody), native status (USDA 2012), and regional status as a potentially 'invasive' exotic (derived from www.invasive.org/south/ and www.invasiveplantatlas.org).

As an indicator of hydrology, water depths were measured at each location and assigned qualitative ranks of none, shallow (< 0.5 m), or deep (> 0.5 m) [ranked respectively as 0, 1, 2]. Sampling occurred in late summer, when the absence or presence of water can indicate relative seasonal hydroperiods from shorter to longer duration. Other hydrology indicators (e.g., water lines) were also noted to aid in interpreting wetness conditions (see De Steven and Gramling 2012).

References for plant identification included Radford et al. (1968), Godfrey and Wooten (1981), Godfrey (1988), and Weakley (2010). For consistency, species nomenclature in this paper follows the PLANTS database (USDA 2012, at http://plants.usda.gov).

Data Analysis. The partial linkages among HGM type, prior-habitat status, and restoration approach (non-intensive vs. intensive) were used to classify wetlands for vegetation analysis. Nine riverine projects that used the 'dual-practice' approach were split into sub-areas for the two contrasting intensive treatments (water-managed vs. tree-planted), giving

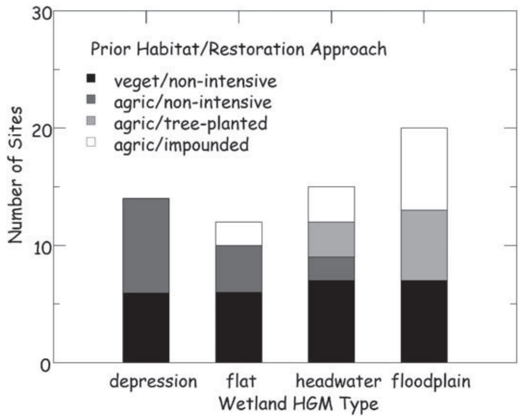

FIG. 1. Distribution of wetland HGM types, pre-restoration habitat conditions (vegetated or agriculture) and 'intensive' (tree-planted or impounded) vs. 'non-intensive' restoration approaches for 61 WRP project sites.

a total of 61 distinct 'sites' for analysis (Fig. 1). These 61 sites were classed into six *a priori* site-groups: depressions (DEPR), flats (FLAT), riverine headwaters (RIV-H), prior-forested floodplains (RIV-F), managed moist-soil impoundments (MSM), and tree-planted headwater and floodplain areas (HF-PT). Sites in the four HGM-defined groups had all been restored non-intensively (Fig. 1). The MSM group included the water-managed areas of prior-cropped floodplains and headwaters, plus two prior-cropped flats that had been modified into managed impoundments. The tree-planted sites (HF-PT) were all associated with prior-cropped floodplains and headwaters. Project age averaged 5–7 years in each group.

Data were compiled over sample locations at each of the 61 sites (1–4 locations per site). Variables characterizing each site included a five-level wetness score (0, 0.5, 1, 1.5, 2) based on the average water-depth ranks, and the relative proportions of native species, hydrophytic species (FAC or wetter), and wetland species (FACW and OBL only). An index of 'floristic quality' (FAQWet4 of Ervin et al. 2006) was also calculated for each site. FAQWet4 uses species wetland-indicator scores ranging from 5 (OBL) to -5 (UPL) combined with frequency-weighted percent nativity; although lacking a fixed range, an index > 0 indicates hydrophytic vegetation and higher values (10–20) suggest a preponderance of native and 'true' wetland species. Differences in the descriptive variables among groups were tested by analysis of variance (ANOVA) in SYSTAT® (SPSS, Inc.), using Tukey's tests for group-mean comparisons. Diagnostics did not indicate any substantive departures from model assumptions, but the arcsine-square root transformation was applied generally to proportion data to improve homogeneity of variances.

Site floristic composition was analyzed with non-metric multi-dimensional scaling (NMS), multiple-response permutation procedures (MRPP), and indicator species analysis (ISA) in PC-ORD™ (McCune and Mefford 2011). The species data were counts per site, averaged over sample locations and strata. To reduce data noise and improve analytical stability, we merged some highly similar species to generic level (mainly in speciose taxa such as *Cyperus* and *Juncus*) to obtain 318 taxa from 384 species, and then omitted very infrequent taxa found in only 1–3 sites ($\leq 5\%$ of sites; cf. McCune & Grace 2002). A 3-dimensional NMS ordination was identified as optimal (final stress = 15.3), with site-scores rotated to principal axes for display in the 2 main dimensions. Possible explanatory variables were tested for Pearson correlation with the ordination scores. These variables included wetness score, FAQWet4 index, percent non-native species, project age, and number of vertical strata present (from 1–3 for herb, herb + sapling, herb + sapling + tree) as an indicator of overall vegetation structure. Significant ($P < 0.05$), non-redundant variables were displayed as vectors in the ordination graph. MRPP tested whether the six site-groups accounted for more compositional variation than if sites were classed only into four HGM types; lower (more negative) values of the *T*-statistic indicate stronger group separation (McCune and Grace 2002). MRPP was also used to test whether composition differed generally with prior-habitat status (agriculture *vs.* vegetated). The ISA was conducted on the same data matrix, where species indicator values (I.V.) are calculated as the product of relative abundance and relative frequency in a given group compared to all groups (McCune and Grace 2002). Indicator species for site-groups were tabulated as those species having an I.V. significant at $P < 0.10$, which detected taxa that contrasted more than one group jointly from other groups.

Table 2. Habitat and vegetation traits of 61 WRP sites in six site-groups: MSM (moist-soil managed), DEPR (depression), FLAT (flat), RIV-H (riverine headwater), RIV-F (riverine forested floodplain), HF-PT (tree-planted headwater or floodplain). Indicator taxa are from ISA at $P < 0.10$. Site traits are means ± SE. ANOVA d.f. = 5, 55; ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$, or n.s. (not significant).

Descriptor or trait	MSM	DEPR	FLAT	RIV-H	RIV-F	HF-PT	ANOVA Sig.
GROUP DESCRIPTORS							
Sites in group (n)	12	14	10	9	7	9	—
Prior-agriculture sites (% of n)	100	57	40	22	0	100	—
Indicator taxa (number per group)	12	2	3	7	21	12	—
SITE TRAITS ‡							
Wetness score (0–2)	1.2 ± 0.1^{D}	0.7 ± 0.2	0.2 ± 0.1	0.4 ± 0.1	0.7 ± 0.1	0.06 ± 0.06^{D}	**
Vegetation strata (1–3)	1.0 ± 0.0^{D}	1.8 ± 0.2	2.2 ± 0.2	2.4 ± 0.2	3.0 ± 0.0^{D}	2.1 ± 0.1	**
FAQWet4 Index	13.2 ± 1.1	9.9 ± 1.4	8.8 ± 1.6	9.2 ± 1.1	14.1 ± 2.2	6.0 ± 1.1^{D}	**
Hydrophytic species (%)	98.0 ± 0.8^{D}	86.2 ± 3.4	89.2 ± 3.5	84.9 ± 2.1	92.6 ± 2.6	80.1 ± 2.3^{D}	**
Wetland species (%)	90.3 ± 2.8^{D}	63.5 ± 6.4	54.6 ± 6.7	53.7 ± 4.0	61.3 ± 5.7	48.8 ± 5.3	**
Herbaceous species (%)	81.5 ± 3.4^{D}	54.8 ± 5.9	39.4 ± 7.9	45.7 ± 3.9	32.8 ± 3.6	47.7 ± 3.0	**
Annual species (%)	20.2 ± 5.1^{D}	3.6 ± 1.5	3.7 ± 1.2	7.2 ± 2.3	1.6 ± 0.8	2.6 ± 1.3	**
Native species (%)	93.8 ± 2.3	95.0 ± 1.9	96.2 ± 1.7	92.0 ± 2.0	98.5 ± 1.1	93.9 ± 2.1	n.s.
Non-native species (number)	1.0 ± 0.4	0.9 ± 0.4	0.9 ± 0.5	2.4 ± 0.6^{D}	0.4 ± 0.3	1.3 ± 0.5	†
'Invasive' non-natives (number)	0.08 ± 0.08	0.4 ± 0.2	0.6 ± 0.3	1.6 ± 0.4^{D}	0.3 ± 0.2	0.8 ± 0.3	*

‡ for each trait, D superscript indicates group means that differ from each other and from all remaining group means in the row.

Results. General Vegetation and Habitat Traits. The intensively restored MSM and HF-PT sites differed in general vegetation attributes from each other and from the non-intensively restored groups (Table 2). Both had more distinctive indicator taxa than most other groups except forested floodplains (the least altered habitats). MSM sites were the wettest, with the highest proportion of hydrophytic and wetland species and the highest FAQWet4 values. These moist-soil managed sites were typically inundated and had mostly herbaceous species, including many wetland annuals. In contrast, HF-PT sites were comparatively the driest, with relatively fewer hydrophytic and wetland species and lower FAQWet4 values. These tree-planted headwaters and floodplains had a midstory stratum of the young planted trees plus a variety of other woody and herbaceous species.

The MSM and HF-PT sites were all prior-agriculture by definition. Excepting prior-forested floodplains (RIV-F), sites in the other three HGM-defined groups had a mix of prior-habitat and wetness conditions, yet the four groups were similar in most general attributes except for differences in vegetation structure (Table 2). RIV-H sites averaged more potentially 'invasive' non-natives, but the mean number of such species per site was low in all groups.

Mean richness of all dominant species (not shown) averaged 23 per site with no substantive between-group differences (cf. De Steven and Gramling 2012). Likewise, all six groups averaged $\geq$ 90% native species and $\geq$ 80% hydrophytic species (Table 2).

Floristic Composition Patterns. MRPP tests confirmed that species composition was differentiated more strongly by the site-groups (n = 6, T = −16.3, $P < 0.0000001$) than by HGM type alone (n = 4, T = −3.2, P = 0.005). The NMS ordination (Fig. 2) showed that the prior-agriculture moist-soil managed sites (MSM) and tree-planted sites (HF-PT) differed floristically from each other and from other groups. A significant overall difference based on prior-habitat condition (n = 2, T = −14.0, $P < 0.0000001$) was largely attributable to the distinctive composition of those two groups (Fig. 2). There was much greater floristic similarity among the four site-groups that had been restored by non-intensive methods.

Site species composition was significantly correlated with site wetness (Fig. 2, vector

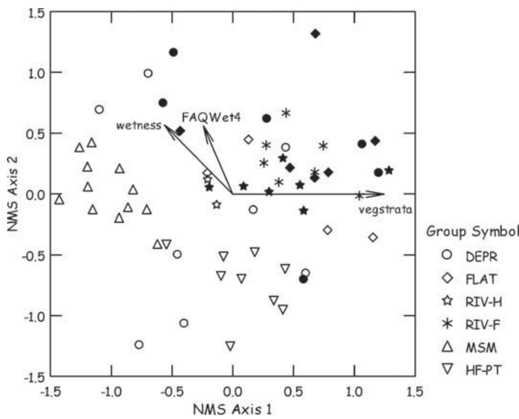

FIG. 2. NMS ordination of floristic composition in 61 WRP sites. Legend shows symbols for six groups (cf. Table 2); filled and asterisk symbols = 'prior-vegetated' sites, unfilled symbols = 'prior-agriculture' sites. Vector arrows show significantly correlated variables, with values increasing from the 0,0 centroid and vector lengths proportional to joint correlation strength.

shown), but not with project age. A major pattern of floristic variation reflected a structural gradient (number of vegetation strata) from simple herbaceous communities to multi-layered forests (Fig. 2, left to right). Floristic quality (FAQWet4) represented a secondary compositional gradient; this partly reflected the prevalence of herbaceous wetland species in MSM and some wetter DEPR sites, *versus* greater frequency of facultative and upland species in HF-PT and some drier DEPR sites. With a range of wetness and prior-habitat conditions, DEPR and FLAT sites varied in structure from open-emergent to shrubby or forested, and they had substantial floristic overlap with each other and with headwater sites (RIV-H) and prior-forested floodplains (RIV-F). The wooded RIV-H and RIV-F sites were very similar in species composition.

Some common taxa that accounted for floristic differences among groups are listed in Appendix 1 (see USDA 2012 for nomenclature authorities). Typical plants in MSM sites were semi-aquatic and wetland forbs and sedges/rushes such as *Hydrolea quadrivalvis*, *Polygonum hydropiperoides*, *Ludwigia* spp., *Cyperus* spp., and *Eleocharis* spp., with *Salix nigra* as a woody colonizer. Many common MSM-site taxa also occurred in DEPR sites, but depressions were distinguished by several perennial grasses (the semi-aquatics *Panicum hemitomon* and *Leersia hexandra,* or the facultative *Dichanthelium acuminatum*) and/or various woody species including *Taxodium ascendens* and *Liquidambar styraciflua*. Most FLAT sites had a variety of herbaceous and woody taxa, particularly trees such as *Acer rubrum, Nyssa biflora*, *T. ascendens*, *Diospyros virginiana*, and *L. styraciflua.* RIV-H sites (nearly all prior-vegetated) shared many taxa with the timber-harvested RIV-F sites, which were dominated by bottomland trees (e.g., *Quercus laurifolia*, *T. distichum*, *N. biflora*, *L. styraciflua*) and native woody vines (e.g., *Ampelopsis arborea, Campsis radicans, Smilax* spp., *Vitis rotundifolia*). With the driest conditions (cf. Table 2), HF-PT sites were distinctly characterized by certain old-field successional herbs and shrubs (e.g., *Solidago* spp., *Symphyotrichum dumosum*, *Andropogon virginicus*, *Baccharis halimifolia*, *Lonicera japonica*, *Rubus* spp.) in addition to the planted bottomland trees (*Quercus* spp., *Fraxinus pennsylvanica*, *T. distichum*) and other volunteer trees (e.g., *Platanus occidentalis*, *L. styraciflua*). That composition contrasted the tree-planted sites from the wetter MSM impoundments that were co-located on the same tracts.

Of the 384 total species recorded as dominants, 31 (8%) were non-native. Most of these were naturalized old-field grasses and forbs (e.g., *Bromus japonicus, Cynodon dactylon, Festuca pratensis, Paspalum* spp., *Ipomoea* spp., *Verbena brasiliensis*), thus non-natives occurred somewhat more frequently in prior-agriculture sites (63% of sites) than in prior-vegetated sites (46% of sites) (chi-square test, d.f. =1, n.s.). Ten non-natives of various growth habits were species listed as regionally invasive, though not necessarily in wetlands (Table 3). The two most common were *Lonicera japonica* (Japanese honeysuckle) and *Ligustrum sinense* (Chinese privet). *L. japonica* was a dominant in 13 sites and seen in 3 other sites. *L. sinense* was a dominant in 6 sites and seen in 6 other sites (*Note*: the total of 12 for *L. sinense* corrects an erroneous value of 15 in De Steven and Gramling 2012). Other invasives such as *Alternanthera philoxeroides* (alligator-weed), *Microstegium vimineum* (Japanese stilt-grass), and *Triadica sebifera* (Chinese tallow) were recorded sporadically in 1–3 sites each.

Discussion. The plant data revealed broad floristic patterns that reflected the diverse species assemblages of Southeastern U.S.

Table 3. Potentially 'invasive' exotics recorded in WRP sites. Data for each species are number of sites of occurrence, by wetland group (codes in Table 2). Shown at bottom are the percentages of sampled sites per group with a non-native present, and with an invasive present.

Species	Growth habit	MSM	DEPR	FLAT	RIV-H	RIV-F	HF-PT
Alternanthera philoxeroides	forb‡	1			2		
Ligustrum sinense	shrub		1	1	2	1	1
Lonicera japonica	woody vine		4	2	3	1	3
Lygodium japonicum	vine						1
Melia azedarach	tree		1	1			
Microstegium vimineum	grass				3		1
Rosa multiflora	shrub				1		
Sorghum halepense	grass				1		1
Triadica sebifera	tree			1	2		
Wisteria sinensis	woody vine			1			
% of sites with an exotic	–	50.0	57.1	40.0	88.9	28.6	66.7
% of sites with an 'invasive'	–	8.3	28.6	30.0	77.8	28.6	55.6

‡ semi-aquatic species.

wetlands. Most restored WRP sites had general attributes indicative of functional wetland vegetation (see also De Steven and Gramling 2012); however, they had variable species composition with over 380 species recorded as within-site dominants. Composition was partly influenced by substantial variation in site wetness that represented inherent differences in hydrodynamics; these differences were evident despite summer drought conditions that occurred during the survey year. As hypothesized, floristic composition was also shaped by interactions among wetland HGM type, prior habitat condition (reflecting land-use history), and restoration approaches.

The natural plant communities of Southeastern wetlands are very dynamic, owing to a large regional pool of wetland species and to hydrologic variability that is influenced by HGM settings (see Christensen 2000, and review in De Steven and Lowrance 2011). The result is that wetland types may differ in vegetation structure but overlap considerably in species composition. Riverine headwater and floodplain wetlands typically become forested, since flooding regimes are seasonal in relation to surface runoffs, overbank flows, and microtopographic features that vary with position in the watershed. The natural vegetation of depressions and flats varies more widely; it can range from open-emergent ponds to forests according to individual differences in annual hydroperiods (from semi-permanent to temporary) and susceptibility to fire.

In the WRP sites restored by low-intensity methods, patterns of species composition resembled those of comparable natural wetlands, although at a younger successional age. Most of the restored riverine-headwater sites were seasonally flooded woody wetlands developing toward forest. Likewise, the timber-harvested floodplains experienced natural river flooding and had well-developed forest regrowth. Restored depressions and flats had differing vegetation related to a range of wetness conditions that reflected different hydroperiods. Depression, flat, and headwater groups were not strongly differentiated by prior-habitat status, apart from an unsurprising trend for more frequent presence of non-native species in agricultural sites. Possibly the prior-agriculture wetlands had not been drained or farmed so intensively that they lacked wetland species before restoration; if so, then remnant wetland plants could have recolonized from seed banks or refuge areas, making those sites more similar to prior-vegetated wetlands that perhaps were abandoned from use at a much earlier time.

The distinctive vegetation of moist-soil managed areas and tree-planted floodplains and headwaters was linked to use of active restoration practices to compensate for an intense agricultural history. Typically, these larger tracts had been in continuous row cropping and were isolated hydrologically by small flood-control levees or stream deepening for drainage. Consequently, restoration methods were similar to those used on marginal farmlands in the adjacent region of the Southern Mississippi Alluvial Valley (Haynes 2004, King et al. 2006, Faulkner et al. 2011). In both cases it has been impractical to remove the flood-control levees; instead, restoration uses dikes, water-control structures, and/or excavated swales to create ponded areas at lower elevations, plus widespread reforestation on the higher ground. These practices are also driven by specific WRP objectives for creating waterfowl habitat and recovering bottomland-hardwood forest in these floodplain settings (King et al. 2006). The moist-soil impoundments provide distinctive open-water wetland habitat, with periodic management that maintains early-successional emergent vegetation having more wetland annuals than would occur in mature wetlands. Conversely, lacking reconnection to major riverine flows, the tree-planted sites tend to be drier than natural forested floodplains and have an understory vegetation similar to moist old-fields (see Battaglia et al. 2002). Despite that hydrologic difference, active tree-planting and natural tree recruitment are addressing the habitat goals to accelerate forest development and develop a woody assemblage that resembles the overstory component of floodplain forests (see also King et al. 2006).

Implications. Wetland restoration efforts often seek to replicate historic plant communities, hence success is evaluated by floristic comparison to natural ('reference') wetlands. However, relying strictly on compositional criteria and reference types can be problematic for various reasons (National Research Council 2001, see also De Steven et al. 2010). As we have shown previously (De Steven and Gramling 2012), guild-based attributes (e.g., representation of wetland species, native species, and growth forms) can provide important supplemental data for assessing whether WRP wetlands have recovered desired functions and structure in relation to project goals.

Replicating specific plant communities is not an explicit goal for WRP projects, so deviation from 'reference' floristics does not necessarily indicate an unsuccessful restoration. Of the common species that characterize natural depression, flat, and riverine wetlands (see Wharton et al. 1982, Sharitz and Gibbons 1982, Richardson and Gibbons 1993, Sharitz and Mitsch 1993, Rheinhardt and Rheinhardt 2000, Kirkman et al 2000, De Steven and Toner 2004), 80–90% occurred in non-intensively restored WRP wetlands of the same type (tabulations not shown). About 50% of those characteristic species occurred in the intensively restored WRP sites; however, that difference is related not only to prior land-use but also to the use of methods that favor species associated with active vegetation management (e.g., wetland annuals) or constrained hydrologic recovery (e.g., old-field herbs). Other wetland species that we observed in the WRP sites likely also occur in natural wetlands of all types, but are merely unreported in the limited reference datasets. Since the WRP wetlands will be maintained within a matrix of private working lands, some floristic differences from natural wetlands would be expected, depending on the wetland-management practices used and the extent of upland buffer habitat on the easement. Further monitoring would be needed to determine if the WRP wetlands can retain their compositional variety over the long term.

The study findings also suggest how geographic differences in land-use and climate might influence the plant diversity of restored wetlands on working lands. In the farming-intensive U.S. Central Plains region, prairie-pothole and playa wetlands that are restored under USDA programs do not seem to adequately recover native plant diversity (Smith and Haukos 2002, Aronson and Galatowitsch 2008). Their vegetation becomes more homogenized over time and is frequently dominated by undesirable exotics. Such wetlands often were severely damaged by cultivation and are isolated from remnant natural wetlands that might be sources of plant recolonization; the semi-arid Plains climate also results in drier wetlands that are more susceptible to colonization by invasive exotics (O'Connell et al. 2013). In contrast, within the mixed forested-agricultural Southeast U.S. region, the WRP enrolls wetlands with a range of prior conditions and wetland types; the landscape is richer in nearby source wetlands and the humid climate favors wetter hydrologic regimes. These conditions appear to promote more successful recovery and a greater variety of wetland plant communities, except where hydrologic restoration has been inadequate (cf. De Steven and Lowrance 2011, De Steven and Gramling 2012). Non-native species are sometimes present but rarely dominate a site; many are likely to decline over time as sites mature (e.g. McLane et al. 2012). The net result is that most Southeastern wetlands restored in the Wetlands Reserve Program are currently supporting a range of native plant assemblages that are shaped by multiple factors including hydrogeomorphic settings, variable site history, and restoration approaches linked to specific programmatic goals.

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Appendix 1. Differentiated table of relative Indicator Values (%) for frequent taxa in six WRP groups; + = present but I.V. < 10%. Groups are MSM = moist-soil managed, DEPR = depression, FLAT = flat, Riv-H = riverine headwater, Riv-F = riverine forested floodplain, HF-PT = tree-planted headwater or floodplain. Significant indicator taxa are noted by * $P \leq 0.05$ or † $P < 0.10$.

Taxon	Wetland indicator class	Growth habit	Wetland site-group						ISA Sig.
			MSM	DEPR	FLAT	Riv-H	Riv-F	HF-PT	
HERBACEOUS TAXA									
Ludwigia peploides	wetland	forb ‡	50						*
Hydrolea quadrivalvis	wetland	forb ‡	61		+				*
Eleocharis (6 spp.) §	wetland	rush	28	+	+	+			*
Cyperus (9 spp.) §	wetland	sedge	39	+	+	+	+		*
Diodea virginiana	wetland	forb	33					+	*
Ludwigia (*palustris, spathulata*)	wetland	forb	36	+			+	+	*
Ludwigia (8 erect-form spp.) §	wetland	forb	14	10	+	+		+	n.s.
Polygonum hydropiperoides	wetland	forb ‡	35	13		+		+	*
Panicum hemitomon	wetland	grass ‡	+	34	+				*
Leersia hexandra	wetland	grass ‡	+	25					*
Dichanthelium acuminatum	facultative	grass		16	+		+		n.s.
Woodwardia (*virginiana, areolata*)	wetland	fern		+	25	+	+		*
Mikania scandens	wetland	vine		+	+	18	10	+	n.s.
Carex glaucescens	wetland	sedge		+	+		27		*
Saururus cernuus	wetland	forb			+		44	+	*
Boehmeria cylindrica	wetland	forb				19	+	17	n.s.
Carex lupulina	wetland	sedge	+			18	+	+	n.s.
Juncus (*effusus, coriaceus*)	wetland	rush	12		+	+	+	30	*
Juncus (11 spp.) §	wetland	rush	+	11		+	+	15	n.s.
Carex frankii	wetland	sedge				+		49	*
Andropogon virginicus	upland	grass		+	+			44	*
Symphyotrichum dumosum	facultative	forb		+				71	*
Solidago altissima/gigantea	upland	forb						85	*
WOODY TAXA									
Taxodium ascendens	wetland	tree		15	14				n.s.
Morella cerifera	facultative	shrub		+	10	+	+		n.s.
Diospyros virginiana	facultative	tree		+	19	16	+	+	n.s.
Acer rubrum (Coastal-Plain)	wetland	tree		+	24	16	29	+	*
Nyssa biflora	wetland	tree		+	11		11		n.s.
Toxicodendron radicans	facultative	vine		+	13	25	15	+	*
Smilax rotundifolia	facultative	vine		+	10	+	50		*
Parthenocissus quinquefolia	facultative	vine		+	+	23	14		†
Vitis rotundifolia	facultative	vine		+	+	13	20	+	n.s.
Ampelopsis arborea	facultative	vine	+	+	+	10	26	+	*
Campsis radicans	facultative	vine	+	+	+	+	26	+	*

Appendix 1. Continued.

Taxon	Wetland indicator class	Growth habit	Wetland site-group						ISA Sig.
			MSM	DEPR	FLAT	Riv-H	Riv-F	HF-PT	
Quercus laurifolia	wetland	tree		+		+	39		*
Liquidambar styraciflua	facultative	tree		10	16	13	22	14	n.s.
Salix nigra	wetland	tree	25	+	+	16	+	+	†
Taxodium distichum	wetland	tree	+	+	+		33	+	*
Fraxinus pennsylvanica	wetland	tree	+			+	12	26	*
Baccharis halimifolia	facultative	shrub		+	+	+	+	17	n.s.
Lonicera japonica #	upland	vine		+	+	+	+	13	n.s.
Rubus spp.	upland	shrub		+	+	+		45	*
Quercus phellos	wetland	tree		+	+	+		13	n.s.
Quercus nigra	facultative	tree		+		+	+	23	†
Platanus occidentalis	wetland	tree				+	+	48	*
Quercus (*pagoda, texana*)	wetland	tree						44	*

‡ semi-aquatic species.
§ includes 1 or more annual species.
# non-native, considered 'invasive' in some habitats.